PALEONTOLOGY.—*Paleontologic record of the primary differentiation in some major invertebrate groups.*

David Nicol, George A. Desborough, and James R. Solliday, Southern Illinois University, Carbondale, Ill.

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A table of the geologic ranges of the principal animal phyla, prepared by Shrock and Twenhofel (1953, p. 11), should be of interest to all students of evolution. According to their data, the animal phyla with a good fossil record, those having hard parts that are readily preserved, all appeared by about 450 million years ago, and most of them are still older. In other words, according to present knowledge of the fossil record, the major differentiation of the animal kingdom was completed by about the end of the Cambrian period. Probable exceptions to this, which would now appear to be few in number, would be of two kinds—animal phyla with poor or no fossil records and extinct phyla which are not recognized as such now. At the present state of knowledge it can be said that only many lesser groups—classes, orders, families, and genera—first appeared in time less than 450 million years ago.

This would seem to support the assertion of Willis (1940, p. 186):

> It is clear that the tests give a very strong evidence indeed in favour of the theory of differentiation or divergent mutation, according to which the course of evolution is in the opposite direction to what has hitherto been supposed, and by mutations which tend to diminish as time goes on, but go in the direction family-genus-species. The organism that first represents the family is, of course, at the same time its first genus and species, but these are of different rank from genera and species in a larger family. By further mutations this will then give rise to further genera and species. The first new genus formed will usually be widely divergent from the parent genus of the family, even if the family be quite small, e.g. of two genera only. Later formations will be less and less divergent on the whole, but will show some of the characters of divergence of their first parents. The main lines of divergence are therefore given by the latter, and later genera fill them in, as shown by a good dichotomous key.

This is the main theme in Willis's book, and he repeats it many times in various ways. In another place Willis (p. 191) states: "Evolution goes on in what one may call the downward direction from family to variety, not in the upward, required by the theory of natural selection." Willis attributes the idea of divergent mutation to H. B. Guppy and claims that it was adumbrated by St. Hilaire. More recently James Small (1951, p. 131) has stated the same idea: "The general factual picture of evolution is now one of progressive evolution by apparently large steps for the phyla, combined with diversification of genetic patterns *downwards* from phyla to families, genera, species and lower categories." Schindewolf (1951, p. 139) has stressed divergent mutation, too, as shown by this paragraph:

> Palaeontological evidence suggests that the beginning of each phylogenetic cycle, irrespective of the systematic category concerned, is marked by an intensification of evolution. In the later phases, the rate of evolution is much smaller and the ability to change decreases. An instructive example is the evolution of the placental mammals in the early Tertiary. In the upper Cretaceous the Insectivora appear, initiating the evolutionary cycle of the Eutheria. At the boundary of Cretaceous and Tertiary, and in the early Paleocene all other known placental orders become differentiated from the original group. Twenty-five orders, representing the entire morphological range of the subclass, appear in the relatively short period of 10–15 million years, whilst during the subsequent, post-Paleocene, period of 60 million years not a single new order is added.

Other workers who have favored the theory of early primary divergence could be cited, but the ones either mentioned or quoted herein should suffice to show that this is not a new idea nor is it without its adherents today. The thesis of these workers is that the major subdivisions of a group (e.g., classes of a phylum or orders of a class) generally originate early in its history, whereas new subdivisions of lesser rank (e.g., genera and species) may arise at any time throughout the group's geologic history.

For this paper the writers have taken 13 major invertebrate groups with a good paleontologic record and have recorded the geologic ranges of their primary subgroups. In the case of a phylum, the geologic ranges of its classes were plotted; in the case of a class, the geologic ranges of its orders were recorded; and so on. With these data we hope to show whether the basic pattern of evolution is like that described by Willis and others who claim that primary divergent mutation occurs early in the history of a major group or is like that described by other workers who contend that primary divergences occur as a gradual and steady process throughout the geologic history of each group. The latter idea is conventionally considered the more logical pattern in evolution. Except for some work by Schindewolf almost no analyses of this sort have been attempted by invertebrate paleontologists.

COMPILATION AND PRESENTATION OF DATA

Thirteen examples are presented, all taken from invertebrate groups with a good fossil record. The writers have purposely avoided groups like the Trilobita and the Porifera because so much of the history of their divergence ranges back to the base of the Cambrian that a long pre-Cambrian history might be postulated for both of them even though the direct evidence of the fossil record is scanty or absent. We have avoided groups where the basic classification is not well understood or where the fossil record is rather poor. Our examples are drawn from the following phyla: Protozoa (1), Coelenterata (3), Bryozoa (1), Brachiopoda (1), Mollusca (2), Arthropoda (1), Echinodermata (3), and Protochordata (1). These, we believe, give us a reasonably large sample of the invertebrate phyla, although additional examples could have been obtained.

Another way by which we have attempted to avoid a bias of the data is to exclude the declining phase of a group's evolution—i.e., the phase in which it approaches extinction. For example, we have used only the Paleozoic history of the orders of nautiloids and the superfamilies of articulate brachiopods because the possibility of the occurrence of a primary divergence in a group approaching extinction is remote. However, in the case of the graptolites we have included data on the final stage of the group's existence because the complete geologic history, from inception to extinction, illustrates a typical pattern of rapid evolution.

The first appearance of a particular group is the most important part of the data presented here. No attempt was made to show the phylogenetic relationships of the various groups to each other, for two reasons. The first is that this information is unimportant for our purposes in this paper. Secondly, many of these relationships are not well understood and are a matter of conjecture. The writers do not claim to be experts on the phylogeny of the groups used as examples.

In the presentation of the data concerning the time of origin, only the primary divergences or largest subdivisions of a particular group have been used. In other words, for the phylum Mollusca we have considered only the classes; for the subclass Nautiloidea we have used only the orders.

We are well aware that scientists differ in their opinions concerning the classes which should be included in a particular phylum, the orders which should be included in a particular class, and, in some cases, the question of whether a certain group should be ranked as a class or an order or whether another group should be ranked as an order or a family. For this paper we have excluded aberrant groups for which the allocation is questionable and have sought to avoid excesses of classificational splitting and lumping. In deciding which primary subdivisions to include in each of our major groups we have relied on either the consensus or the latest authority. We have also done this for the data regarding the time of the first appearance of each primary subdivision, in some cases taking the majority opinion from standard textbooks on paleontology and zoology and in others using the most recent authoritative work. Only in the latter cases have we specifically cited the references from which our data were taken.

There is no exact agreement on the time

span, in millions of years, of the various periods of geologic history. We have used the same time scale as was used by Knight (1952, p. 7) with the exception of dividing the Carboniferous into Mississippian and Pennsylvanian periods and combining the Tertiary and Quaternary periods by using the Cenozoic era. Knight stated that his data were taken from *Report of the measurement of geologic time of the Division of Geology and Geography,* National Research Council, for 1949–1950, p. 18. The writers have not seen this latter reference. The chart used by Knight is here reproduced, with few modifications:

Era or period	Duration, millions of years	Occurrence, millions of years ago
Cenozoic	60	0–60
Cretaceous	70	60–130
Jurassic	25	130–155
Triassic	30	155–185
Permian	25	185–210
Pennsylvanian	25	210–235
Mississippian	30	235–265
Devonian	55	265–320
Silurian	40	320–360
Ordovician	80	360–440
Cambrian	80	440–520

DISCUSSION OF COMPILED DATA

The sequence in which the examples are presented is from the groups of organisms that are structurally simpler to the more complex ones. The first example (Fig. 1), therefore, comprises four families of planktonic Foraminifera as compiled by Loeblich and collaborators (1957). These families are generally considered by most micropaleontologists to be phylogenetically related, although there are a few planktonic Foraminifera not included in these four families. In preparing this figure the writers arbitrarily assigned the same amount of time to each of the Cretaceous stages, there being 12 of them if the Danian is excluded as was done by Loeblich and his collaborators. The first family, the Orbulinidae, appeared at the beginning of the Hauterivian stage, approximately 120 million years ago, and continues to the present. At the beginning of the Aptian stage, approximately 12 million years later, two more families emerged—the Globorotaliidae and the Hantkeninidae. These two families also have living representatives. Finally, at the beginning of the Turonian stage, the last of the families arose, the Globotruncanidae, only 30 million years after the first-appearing of these four families. The Globotruncanidae were a relatively short-lived family that became extinct at the end of the Cretaceous. To summarize: within 12 million years three of the four families made their appearance, and within approximately 30 million years all of them had emerged. Thus, all the basic differentiation took place within a time span of 30 million years and no new families have appeared in the last 90 million years.

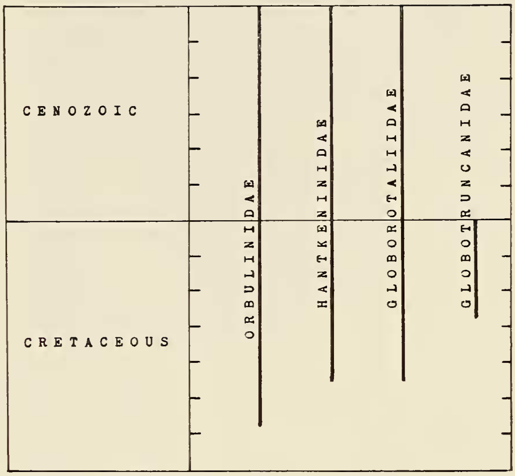

FIG. 1.—Periods of existence of four related families of planktonic Foraminifera. Data taken from Loeblich and collaborators, 1957. Horizontal stubs demark 10-million-year intervals.

The next example (Fig. 2) comprises the families of tabulate corals (data taken from Hill and Stumm *in* Moore, 1956). The first two families of the Tabulata, the Chaetetidae and Syringophyllidae, appeared almost simultaneously at the beginning of the middle Ordovician. Two more families, the Heliolitidae and Halysitidae, made their appearance during the upper part of the middle Ordovician no more than 20 million years later. At the beginning of the late Ordovician the Auloporidae and Favositidae arose; this was no more than 30 million years after the first two families of tabulate corals began their existence. Thus, in approximately 30 million years the basic di-

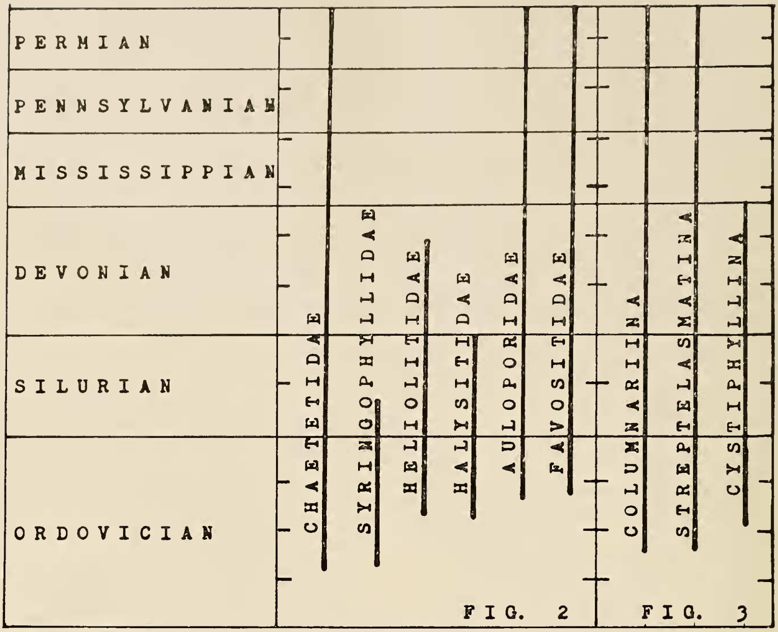

Fig. 2.—Paleozoic history of the families of tabulate corals. Data taken from Hill and Stumm *in* Moore, 1956. Horizontal stubs demark 20-million-year intervals.

Fig. 3.—Periods of existence of the suborders of rugose corals. Data taken from Hill *in* Moore, 1956. Horizontal stubs demark 20-million-year intervals.

vergence of the Tabulata was completed, and no new families appeared throughout the remaining 200 million years of the Paleozoic era.

Many of the major groups studied have included subgroups which existed only briefly, usually early in the history of the major group. For example, the Syringophyllidae, Heliolitidae, and Halysitidae appeared within the first 20 million years of tabulate existence. The Syringophyllidae were extant for about 70 million years, the Heliolitidae for less than 120 million years, and the Halysitidae for about 80 million years. The occurrence of short-lived subgroups is common enough that it should be considered an important phenomenon, although it has been left unexplained in theories on the basic causes of evolution.

The suborders of the rugose corals (Fig. 3) (data taken from Hill *in* Moore, 1956) provide another illustrative example of rapid primary divergence. All three suborders of the Rugosa emerged within about the first 10 million years of the order's beginning in the middle Ordovician. No new suborders appeared during the remainder of the Paleozoic, a span of 220 million years, although many families and groups of lesser rank did arise after all of the suborders had been established.

Another interesting example (Fig. 4) is that of the primary divergence in the scleractinian corals (data taken from Wells *in* Moore, 1956). Three of the five suborders appeared almost simultaneously in the middle Triassic. About 25 million years later the fourth suborder arose in the early Jurassic. Some 80 million years after that, or about 105 million years after the scleractinians began, the last suborder originated in the late Cretaceous. No new suborders have appeared during the 70 million years since. Most of the basic divergence in the scleractinian corals took place within the first 25 million years, and only one new suborder appeared in the last 150 million years of scleractinian history.

Many scientists, particularly in the field of genetics, would expect evolution to be a

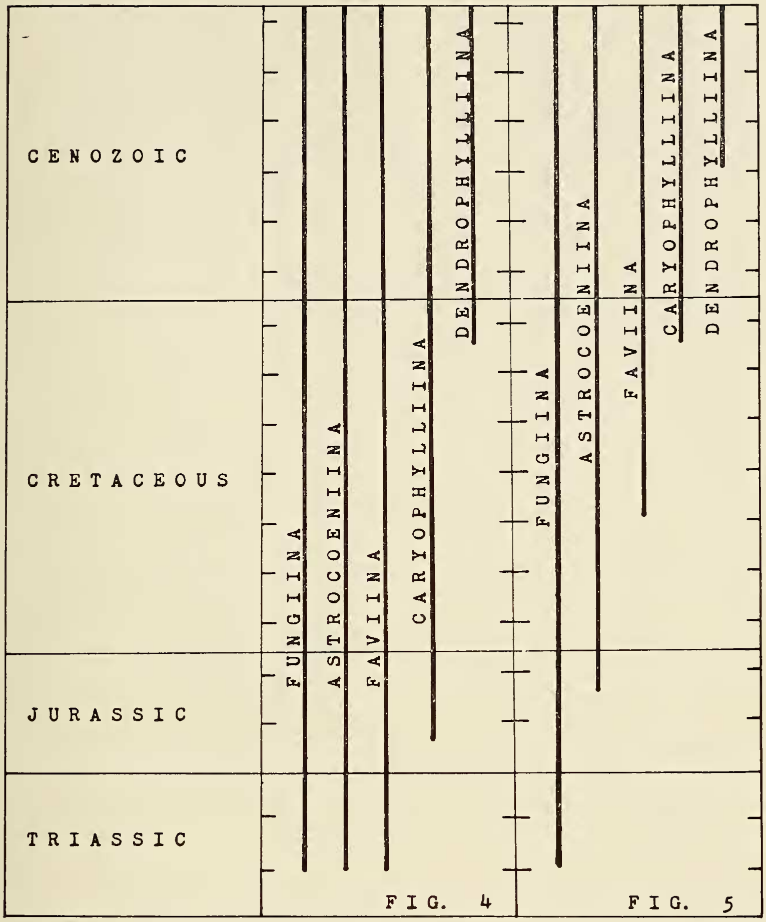

FIG. 4 FIG. 5

Fig. 4.—Periods of existence of suborders of scleractinian corals. Data taken from Wells *in* Moore, 1956. Horizontal stubs demark 10-million-year intervals.

Fig. 5.—Hypothetical periods of existence of suborders of scleractinian corals. If evolution were a slow, gradual, and steady process, with primary divergences occurring at regular intervals throughout geologic history, new suborders of scleractinian corals would have arisen at 35-million-year intervals. Cf. Fig. 4.

relatively steady and gradual process, with primary divergences occurring one by one at regular intervals throughout the history of a major group. We digress here in order to compare the actual paleontologic record of the suborders of the scleractinian corals with the theoretical record which would have been established if this hypothesis were true (cf. Figs. 4 and 5). Assuming that the scleractinian corals have existed for 175 million years, the first suborder having originated at the beginning of the middle Triassic, one might expect the other four suborders to appear thereafter one at a time at 35-million-year intervals (and a new suborder would be due to arise soon). Thus, according to the "regular interval" theory, one suborder would have originated at the base of the middle Triassic, one in the middle Jurassic, one in the early middle Cretaceous, one in the late Cretaceous, and one near the middle Cenozoic. In actual fact, however, the record is remarkably different.

It should be pointed out that the foregoing comparative example is based on a group that evinces little or no indication of decline in evolutionary vigor at the present time. Similar comparisons between actual and theoretical evolution are presented in

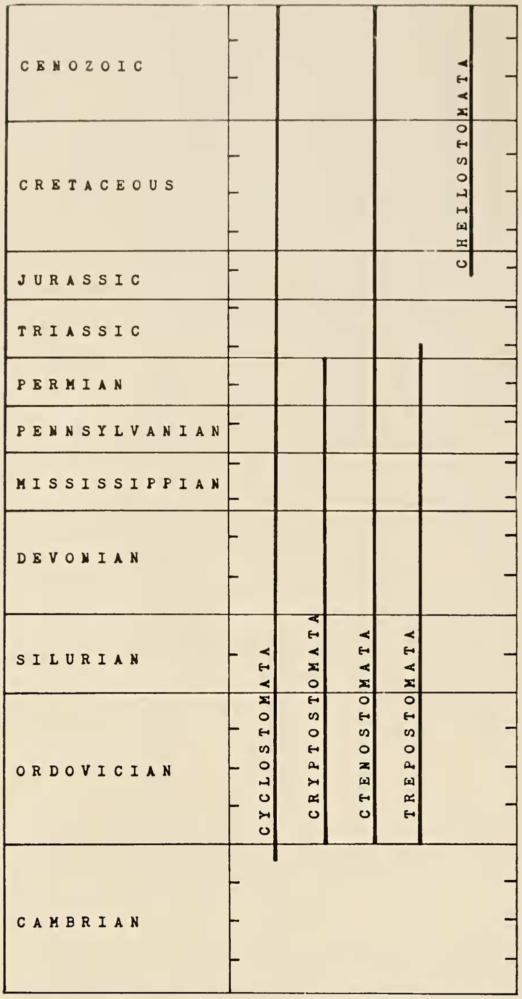

Fig. 6.—Periods of existence of classes of Bryozoa. Horizontal stubs demark 20-million-year intervals.

Figs. 8 and 9, the classes of the Mollusca, and Figs. 12 and 13, the classes of the Echinodermata. These phyla also show no tendency toward extinction at the present time. In all three examples it is clear that major divergences have not occurred gradually or at regular intervals throughout the history of each group.

Returning to the presentation of the basic data, we cite another good case of early rapid divergence: the five classes of the phylum Bryozoa (Fig. 6). Within probably 10 million years during late Cambrian and early Ordovician times, four of the five classes appeared. Not until 310 million years later did the fifth class, the Cheilostomata, make its debut during the late Jurassic. No new classes of the Bryozoa have appeared within the past 140 million years. In other words, most of the basic divergence in the Bryozoa occurred during a brief span of 10 million years; for the past 450 million years, little primary divergence has occurred within the phylum.

The superfamilies of the Paleozoic articulate brachiopods (Fig. 7) also provide a good example of rapid primary divergence. The data were taken from Cooper and Williams (1952, part of fig. 6, p. 332). At the beginning of the Cambrian the Orthacea emerged. No more than 20 million years later, still in the early Cambrian, three more superfamilies began their existence. Two of these, the Rustellacea and the Kutorginacea, were short-lived and became extinct within about 35 million years. Then there was a lag of nearly 80 million years, or 100 million years after the beginning of the Cambrian, before more divergent mutation took place. The Triplesiacea and the Atrypacea appeared almost simultaneously in the middle of early Ordovician time. About 10 million years later two more superfamilies emerged in the late early Ordovician. Some 15 million years after that, five more superfamilies appeared; this was accomplished by middle Ordovician time. During the late Ordovician one more superfamily arrived on the scene, the Productacea. Thus, within a part of the Ordovician period spanning less than 60 million years, 10 new superfamilies appeared. By the middle part of the early Silurian the last two superfamilies began their existence. It took more than 170 million years for all 16 of the superfamilies to emerge. In the remaining 165 million years of the Paleozoic era, no new superfamilies of articulate brachiopods appeared, and, with one possible exception, none arose during the articulate brachiopods' period of decline in evolutionary vigor, the 185 million years represented by the Mesozoic and Cenozoic eras.

The time lag of 80 to 100 million years between the appearance of the first articulate brachiopod superfamilies and the time of rapid divergence which began in the early Ordovician is analogous to the time lag between the inception and the period of rapid

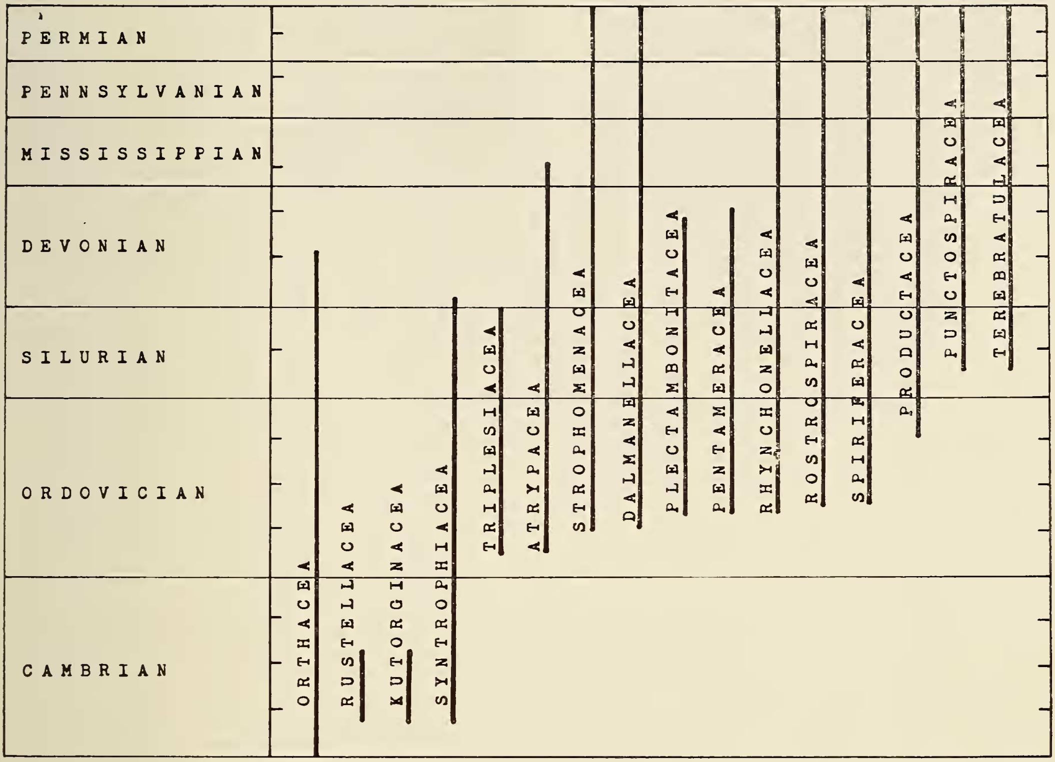

Fig. 7.—Paleozoic history of superfamilies of articulate brachiopods. Data taken from Cooper and Williams, 1952, part of fig. 6, p. 332. Horizontal stubs demark 20-million-year intervals.

emergence of the mammalian orders. As in the case of the mammals, the postponement of rapid divergence of the articulate brachiopods may have been due in part to competition from another group—in this instance the inarticulate brachiopods which flourished first. Another possibility is that the Cambrian seas may have been more suitable for animals with chitinophosphatic shells (e.g., most, but not all, of the inarticulate brachiopods), whereas a favorable environment for animals with calcareous shells (e.g., the articulate brachiopods) did not develop until later. This possibility seems to be confirmed by the fact that many calcareous-shelled animals originated in the early and middle Ordovician (Raymond, 1939, p. 42); examples are the pelecypods, the rugose and tabulate corals, and the bryozoans. Possibly these two factors together may have caused the postponement of rapid primary divergence of the articulate brachiopods.

The classes of the Mollusca (Fig. 8) originated early in the history of the phylum. The gastropods began at the base of the Cambrian. About 60 million years later, in the late Cambrian, the Cephalopoda and the Amphineura appeared. Twenty million years after this latter event, at the beginning of the Ordovician, the Pelecypoda began their existence. Finally, the Scaphopoda emerged at the base of the Silurian, 160 million years after the beginning of the Cambrian, or 80 million years after the appearance of the Pelecypoda. No new classes of Mollusca have emerged during the 360 million years since the beginning of the Silurian. In other words, most of the primary divergence within the Mollusca was accomplished in no more than 80 million years, and it all occurred within a span of 160 million years. All the known classes of the Mollusca are long-lived.

Once again the authors digress, this time to compare the actual history of the ap-

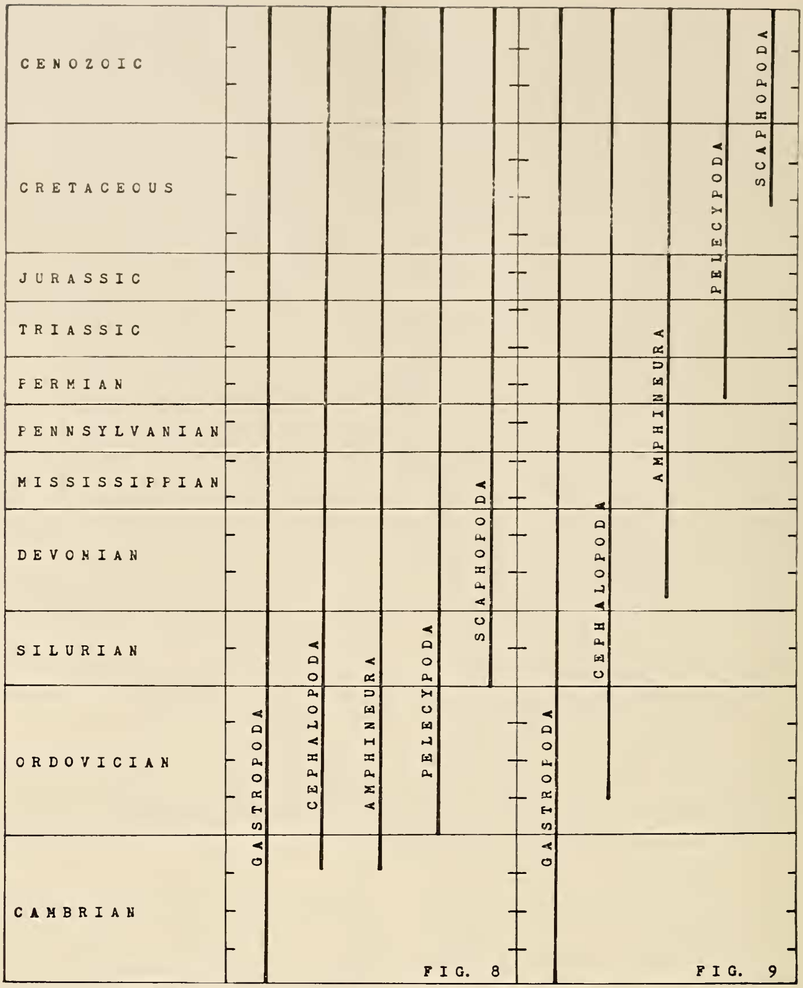

Fig. 8.—Periods of existence of classes of Mollusca. Horizontal stubs demark 20-million-year intervals.

Fig. 9.—Hypothetical periods of existence of classes of Mollusca. If evolution were a slow, gradual, and steady process, with primary divergences occurring at regular intervals throughout geologic history, new classes of Mollusca would have arisen at 104-million-year intervals. Cf. Fig. 8.

pearance of the molluscan classes, based on the paleontologic record, with a hypothetical sequence of divergences based on the idea that the classes should appear at approximately regular intervals throughout the entire history of the phylum. If the time from Cambrian to Recent is taken as 520 million years and the first class originated at the base of the Cambrian, then the next four classes should have emerged one by one at approximately 104-million-year intervals and a new, or sixth, class could be expected to appear soon. Accordingly, one class should have arisen at the beginning of the Cambrian, the next one in the early middle Ordovician, the third near the beginning of the Devonian, another at about the base of the Permian, and the last known one in the middle Cretaceous. That the actual record is sharply different from the hypothetical is illustrated by a comparison of Figs. 8 and 9.

Another case of early rapid divergence (Fig. 10) is seen in the orders of the nautiloids (data taken from Flower and Kummel, 1950, with slight modifications). During the late Cambrian the first order of nautiloids, the Ellesmeroceratida, appeared. Beginning at the base of the Ordovician and extending to the middle Ordovician, a tremendous

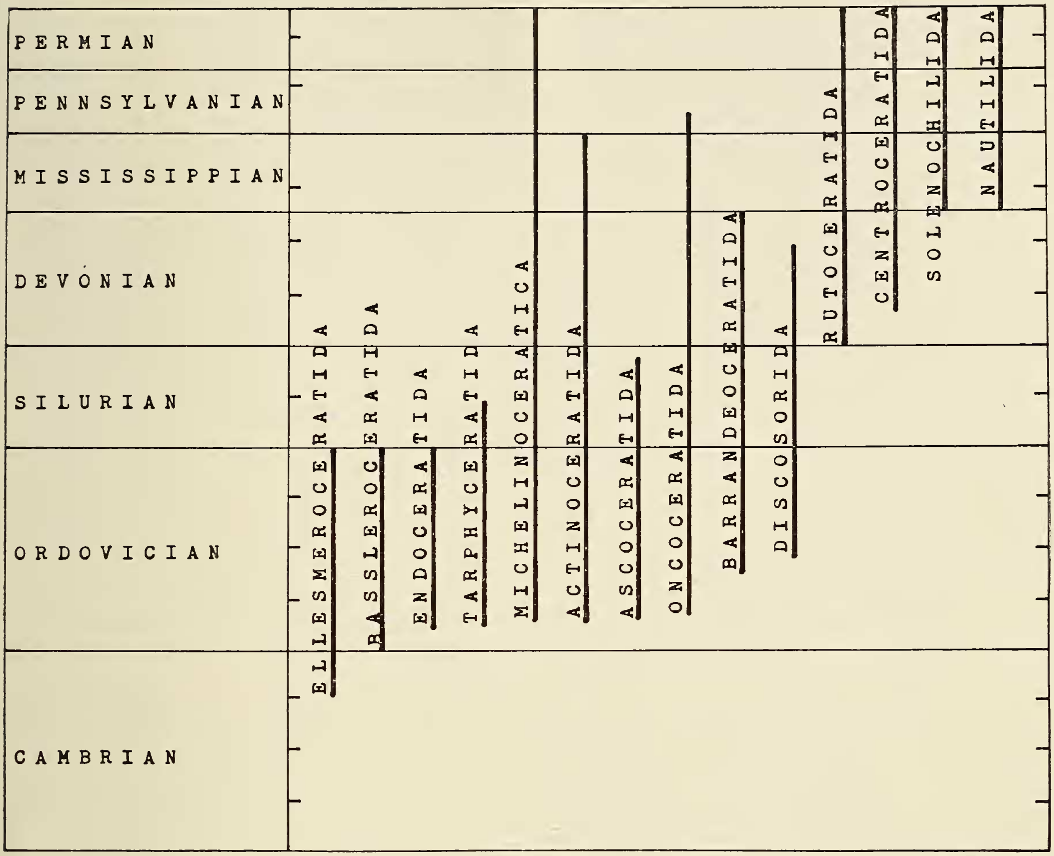

FIG. 10.—Paleozoic history of orders of nautiloid cephalopods. Data taken from Flower and Kummel, 1950, with slight modifications. Horizontal stubs demark 20-million-year intervals.

burst of divergent mutation occurred: within a span of no more than 40 million years, and within about 60 million years of the first appearance of the nautiloids, nine new orders emerged. Several of these were relatively short-lived, having existed for about 100 million years and in a few cases even less. Between 80 and 90 million years later, in the early Devonian, two more orders appeared. Finally, the last two orders arose in the early Mississippian about 195 million years after the beginning of nautiloid history. No new orders of nautiloids emerged during the final 80 million years of the Paleozoic, nor did any appear during the Mesozoic and Cenozoic eras when the general trend of the nautiloids was toward extinction. It is noteworthy that five-sevenths of the nautiloid orders originated within the first one-seventh of the nautiloids' period of existence. In other words, most of the major groups (10 of 14) appeared between the late Cambrian and middle Ordovician. This corresponds well with the time of rapid divergence of many other organisms that had calcareous shells. In the last 400 million years of nautiloid history only four new orders emerged, and even they all began within the first 135 million years of that span of time.

The first superfamily of Paleozoic ostracodes (Fig. 11) emerged at the beginning of the Ordovician period. In the early Ordovician, also, and about 15 million years later, two more superfamilies appeared. About 190 million years after that, the fourth and last superfamily originated; this was at the base of the Pennsylvanian period. During the remainder of the Paleozoic era, 50 million years, no new superfamilies of

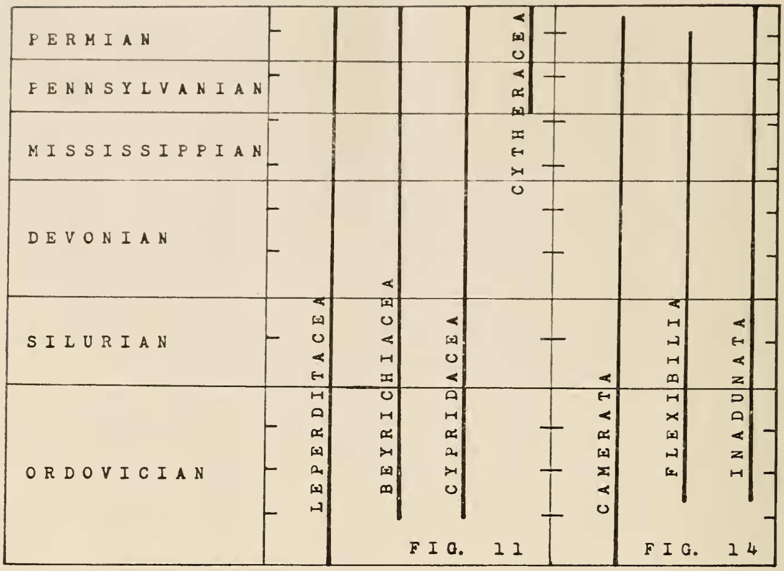

FIG. 11.—Paleozoic history of four superfamilies of ostracodes. Horizontal stubs demark 20-million-year intervals.
FIG. 14.—Paleozoic history of three subclasses of crinoids. Horizontal stubs demark 20-million-year intervals.

ostracodes emerged. Thus, three of the four major groups of ostracodes arose within a span of 15 million years during the early Ordovician, and only one new superfamily appeared during the remaining 240 million years of the Paleozoic era.

In regard to early divergent mutation, perhaps the most illustrative and interesting group studied comprises the classes of the phylum Echinodermata (Fig. 12). The data, collated from several different sources, represent a concensus of authorities. A few questionable groups were not included, as for instance the Bothriocidaroida, which is considered a separate class by Moore (Moore, Lalicker, and Fischer, 1952, p. 577) but not by others, and the classes Cyamoidea and Cycloidea, which are aberrant short-lived middle Cambrian groups and are discussed only by Shrock and Twenhofel (1953, pp. 694–696). If these groups had been included in the present study, the depiction of early divergent mutation among the echinoderms would have been even more striking.

Near the beginning of the Cambrian the Edrioasteroidea appeared, and about 25 million years later, in the middle Cambrian, the Eocrinoidea made their debut. Also in the middle Cambrian, and about 10 million years after the appearance of the Eocrinoidea, the Carpoidea emerged. For the remainder of the Cambrian, about 40 million years, no new classes of echinoderms appeared. At the beginning of the Ordovician, however, three more classes arose. Within the next 40 million years, and no later than middle Ordovician, the Paracrinoidea, Cystoidea, Echinoidea, and Blastoidea made their debut. The Holothuroidea originated in the middle Devonian, no more than 110 million years later than the middle Ordovician. No new classes appeared after the middle Devonian, or for the past 290 million years. Except for the holothuroids, all the classes of echinoderms emerged within the first 120 million years (roughly the first quarter) of the history of the phylum. The most rapid divergence took place within the first 40 million years of the Ordovician period, coinciding again with the time of rapid divergent mutation of many major groups of animals with calcareous skeletons. It is interesting to note here that several of the echinoderm classes were short-lived, having originated and expired early in the history of the phylum.

The writers have chosen the classes of the

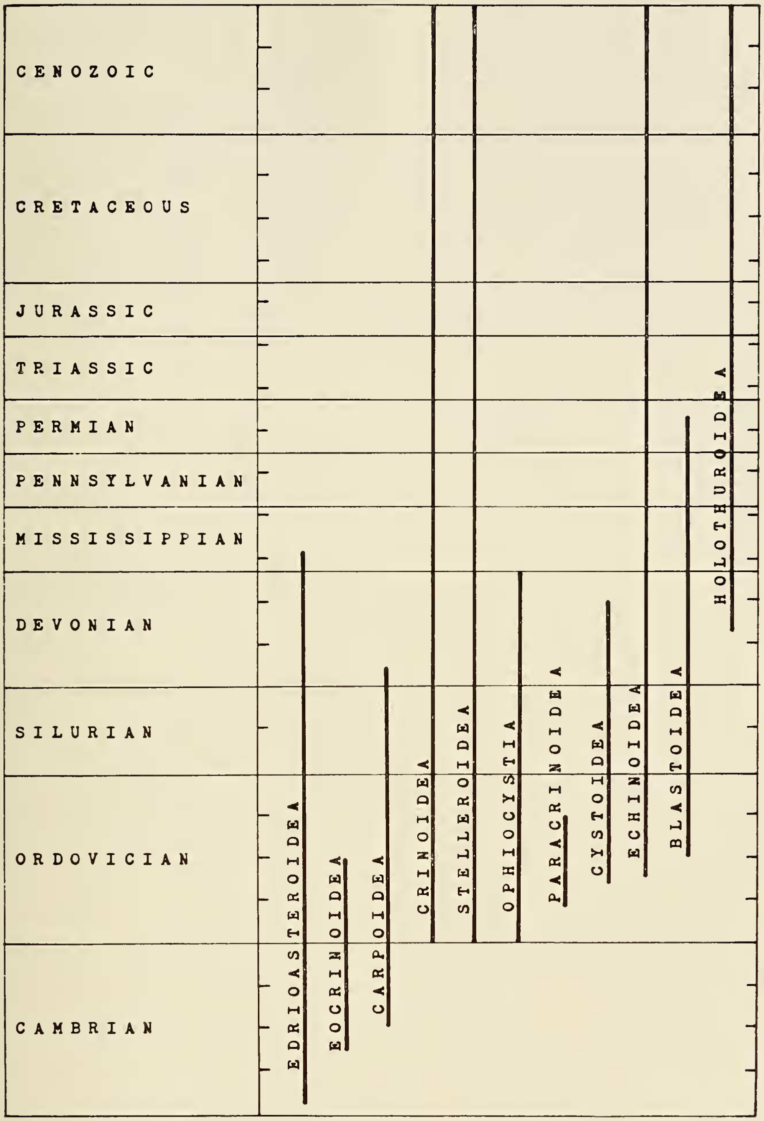

Fig. 12.—Periods of existence of classes of Echinodermata. Horizontal stubs demark 20-million-year intervals.

phylum Echinodermata, a group that shows no evidence of becoming extinct, for presentation of another example of the difference between the actual and hypothetical records of primary differentiation. If we assume that the phylum's history from early Cambrian to Recent spans 520 million years and if we theorize that evolution is a relatively steady and gradual process, the 11 classes of echinoderms should have originated one by one at about 47-million-year intervals. Hence, their individual emergences should have occurred in the (1) base of the Cambrian, (2) middle Cambrian, (3) early Ordovician, (4) late Ordovician, (5) late Silurian, (6) late middle Devonian, (7) latest Mississippian, (8) late Permian, (9) middle Jurassic, (10) middle Cretaceous, and (11) early Cenozoic. The theory appears fallacious, however, when one examines the actual record, which shows that three classes originated before the Ordovi-

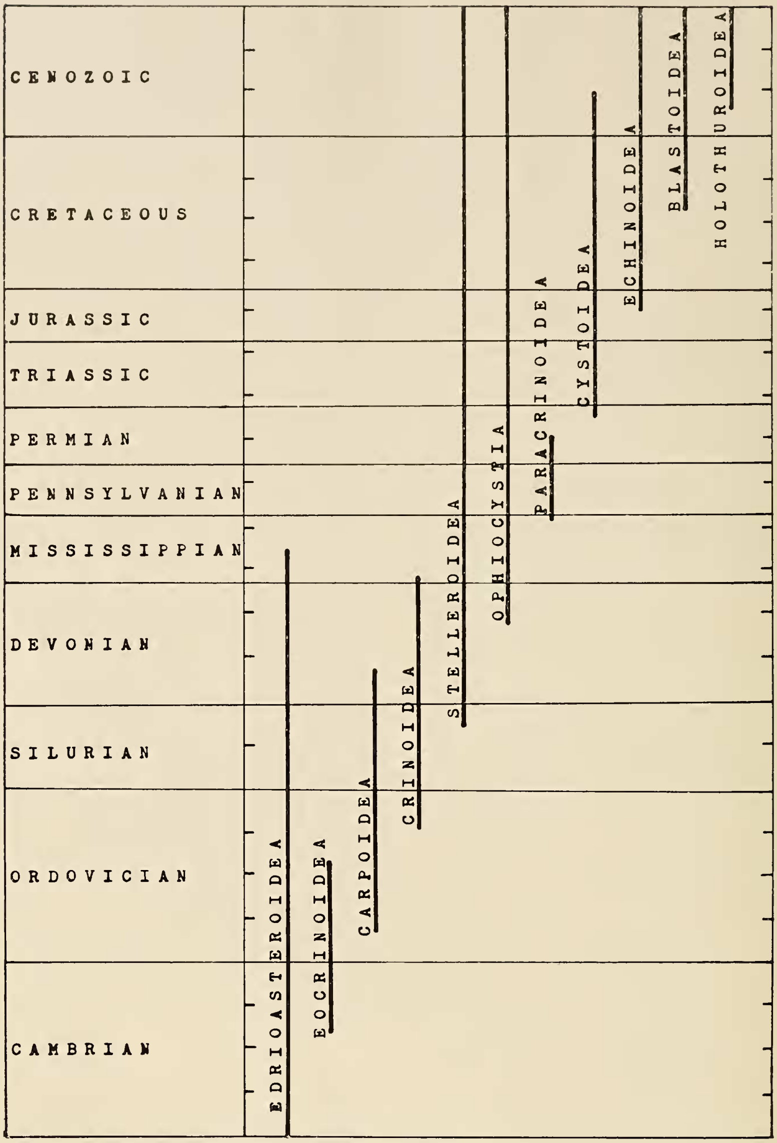

FIG. 13.—Hypothetical periods of existence of classes of Echinodermata. If evolution were a slow, gradual, and steady process, with primary divergences occurring at regular intervals throughout geologic history, new classes of Echinodermata would have arisen at 47-million-year intervals. Horizontal stubs demark 20-million-year intervals. Cf. Fig. 12.

cian, seven during the Ordovician, and only one thereafter. To facilitate comparison we present the actual and theoretical records in Figs. 12 and 13.

The first subclass of Paleozoic crinoids (Fig. 14), the Camerata, appeared at or near the beginning of the Ordovician. No more than 30 million years later, in the early middle Ordovician, the other two subclasses made their debut. Once again we see the early and middle Ordovician as a period of rapid emergence of animals having calcareous shells. For the remainder of Paleozoic time, about 225 million years, no new subclasses of crinoids arose.

The orders of the irregular echinoids are an excellent case of adaptive radiation and rapid divergent mutation (Fig. 15). As soon as the echinoids developed the ability to thrive on a sandy or muddy substrate, they

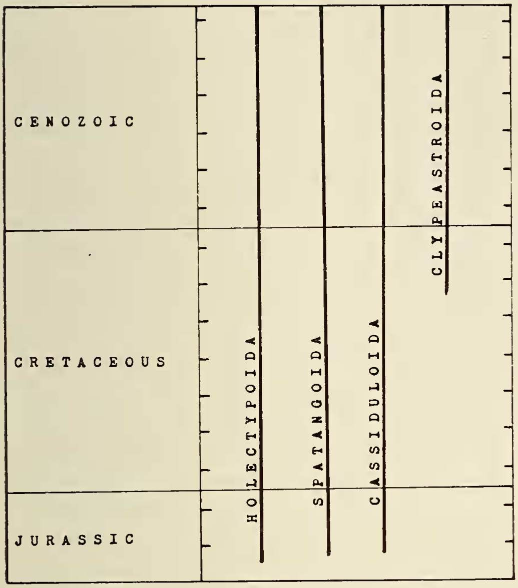

FIG. 15.—Periods of existence of orders of irregular echinoids. Horizontal stubs demark 10-million-year intervals.

evolved quickly. The first order, Holectypoida, appeared in the early Jurassic. Two more orders sprang into existence almost simultaneously in the early Jurassic, probably no more than two million years later. The last order, the Clypeastroida, did not emerge until the late Cretaceous, about 70 million years later. For the past 80 million years no new orders of irregular echinoids have arisen. Most of the primary divergent mutation occurred within the first two million years of the existence of the irregular echinoids; only one new order arose during the subsequent 150 million years.

The five orders of graptolites (Fig. 16) give an excellent and typical picture of the entire history, from inception to extinction, of a rapidly evolving group of organisms. The Dendroidea appeared first in the middle Cambrian. About 25 million years later, in the late Cambrian, the Graptoloidea arose; and approximately 10 million years after that, at the beginning of the Ordovician period, the other three orders began their existence. Two of the latter three orders were short-lived, existing for less than 30 million years. All of the basic divergence within the graptolites was accomplished in about 35 million years. In the remaining 185 million years of graptolite existence, no new orders appeared.

The history of the graptolites can be divided into three phases such as Schindewolf (1951, p. 139) has depicted for other groups of animals. The first phase of rapid divergent evolution (typogenesis) occurred in the graptolites from middle Cambrian to the beginning of the Ordovician—approximately 35 million years—and was characterized by the origin of all of the orders. The second phase (typostasis), or the acme of development of graptolites from the standpoint of numbers of families, genera, and species, occurred during the Ordovician and Silurian periods, or in about 120 million years. This second phase was marked not only by the origins of new families, gen-

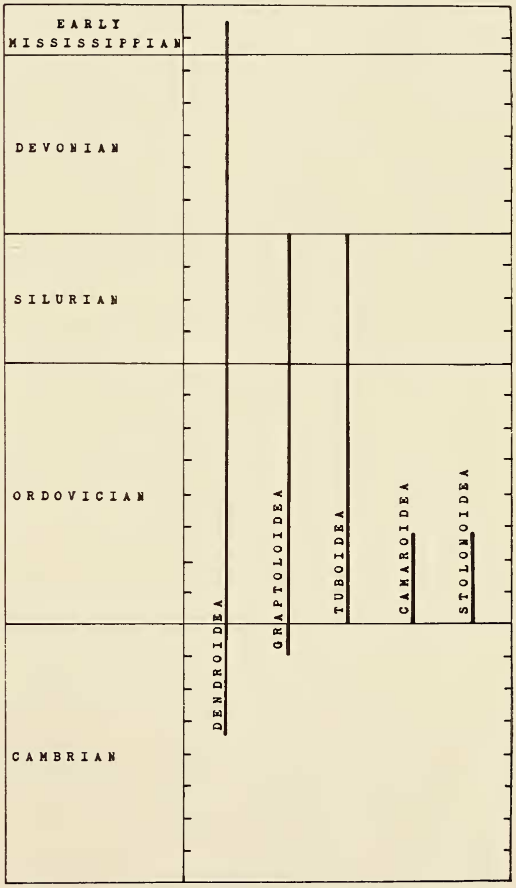

FIG. 16.—Periods of existence of orders of graptolites. Horizontal stubs demark 10-million-year intervals.

era, and species but by the extinction of others. Finally, in the third phase (typolysis) the numbers of lesser subgroups declined and the graptolites became extinct. This last phase occurred during the Devonian and early Mississippian and spanned 65 million years. The senior author (1954, p. 24) has shown that a similar cycle of development, on a much smaller scale, occurred in the long-lived pelecypod species *Glycymeris americana* with regard to its populations and variations.

INFERENCES AND CONCLUSIONS

Believing that the 13 examples used in this study are representative of major invertebrate groups, the authors observe that primary divergent mutation typically occurs early in a group's history, as diagrammed by Schindewolf (1950, p. 239). Thus, the origin of a phylum is closely followed by the origin of all its classes; the inception of a class is soon followed by the inception of all its orders; and a new order is quickly completed in terms of its families. An occasional major divergence may occur much later than the others, but this is rather exceptional. These observations are at variance with the theory that primary differentiation occurs gradually and at regular intervals throughout the history of a given group. That the latter contention is fallacious is graphically demonstrated by a comparison of Fig. 4 with 5, 8 with 9, and 12 with 13, depicting the actual and theoretical histories of the suborders of the scleractinian corals and the classes of the Mollusca and Echinodermata.

One possible explanation for early primary divergent mutation within a major group of animals is alluded to in a somewhat different aspect by Simpson, Pittendrigh, and Tiffany (1957, p. 588). In discussing the appearance of the amphibians they have this to say:

> It is characteristic of evolution that the amphibians did not evolve from late, specialized, progressive or perfected osteichthyans, such as the teleosts, but from primitive forms that lived near the beginning of osteichthyan history. It has usually been true that when a radical adaptive change occurs and a new major group arises, it originates from primitive and not from advanced members of the ancestral group. With progressive adaptation to any one way of life, there often comes a time when the adaptation seems to become irrevocable—a special aspect of the irrevocability of evolution in general. Then change to a radically different way of life becomes, if not impossible, at least extremely improbable.

For example, suppose that the Cephalopoda arose from the Gastropoda: this must have occurred, if at all, early in gastropod history, while the gastropods were still primitive and relatively unspecialized, because later representatives of a major group are generally too specialized to give rise to another group of equal rank. The actual case is that the Cephalopoda did emerge in the first one-eighth of gastropod history, during the time that the gastropods still had primitive or unspecialized representatives.

A fairly common phenomenon is the occurrence of aberrant short-lived subgroups such as two orders of graptolites, several classes of echinoderms, three families of tabulate corals, several superfamilies of articulate brachiopods, and several orders of nautiloids. In most, but not all, cases these short-lived subgroups were among the earlier divergences of their respective groups. If the taxonomic rank assigned to these subgroups is correct on the basis of morphology, then several interesting inferences can be drawn. First: knowing that extinction of families, orders, and classes is not uncommon, one might reasonably assume that extinction of phyla is also not uncommon. The type of geologic history could be the same, in which case extinct phyla may well be more numerous than paleontologists have heretofore acknowledged. Thus, when dealing with aberrant groups which can be only doubtfully allocated to extant phyla, perhaps taxonomists would be more accurate in assuming that they represent extinct phyla. With little confidence and less evidence, paleontologists have allocated aberrant groups such as the conulariids, stromatoporoids, labechiids, receptaculitids, and pleosponges to phyla which still have living representatives; but the fossil groups are sufficiently different from modern groups that such allocations may be erroneous and the extinct groups may actually represent extinct phyla.

It should be stressed, however, that not all extinct groups do represent extinct phyla, no matter how difficult their proper allocations to extant phyla may be. A class of fossil animals having structurally simple hard parts may be so lacking in distinctiveness that its phyletic assignment is dubious; and yet, if the soft parts were available for examination, all doubt would be removed. Moore (Moore, Lalicker, and Fischer, 1952) makes an excellent point when he states (pp. 273–274): "The scaphopods hold unquestioned status as members of the Mollusca in good standing, but if they were known only as fossils, it is certain that they would be put on an *incertae sedis* (uncertain classification) list."

Let us further explore the possibility that extinct phyla may be fairly numerous. The extinction of a phylum of course implies the extinction of all its classes. Conversely, the survival of other phyla implies the survival of at least some of their classes and occasionally the inception of new classes. Considering extinctions, survivals, and new inceptions, one is led to wonder whether there were more phyla and classes of living invertebrates at any one time in the past than there are today. In the case of the echinoderm and bryozoan classes, to cite but two examples, there is no doubt. One has only to look at Figs. 6 and 12 to see that these phyla had more classes of living representatives in the Paleozoic era than in the present. Yet these phyla do not appear to be approaching extinction. That is to say, despite a net reduction in the number of classes, the echinoderms and bryozoans are still flourishing and may actually have more genera and species today than at any other moment of history.

Although they may represent fewer classes and phyla, we would be inclined to believe that there are as many species, genera, families, and possibly orders of animals and plants living on the earth today as at any specific time in the geological past. When one considers the ecological relationships among plants and animals, one realizes that the appearance of a new species generally provides another ecological niche or habitat for one or more additional species as commensals, symbionts, or parasites. The development of grasses provided impetus to the evolution of mammals; the origin of flowering plants promoted the development of insects; more fundamentally, the emergence of land plants was followed by rapid evolution of terrestrial animals. Furthermore, most non-parasitic animals have parasites living inside or outside their bodies, and many of the parasites are peculiar to one or, at most, a few species of host; and so the origin of a new host species encourages the origin of new parasites. Of course, it follows that the extinction of a species may lead to the extinction of some or all of its commensals, symbionts, and parasites; but we strongly suspect that in the general trend of geologic history the proliferation of some genera has fully offset the decline of others. Accordingly, while there may have been a net decline in the number of major living groups (phyla and classes), there has probably been no net decline in the number of minor living groups (genera and species).

Commenting on extinctions, survivals, and new inceptions of major and minor groups, Simpson, Pittendrigh, and Tiffany (1957, p. 754) state:

> Since the Ordovician innumerable groups have died out, but as they disappeared their places were simply taken over by other groups, generally of more recent origin. Among animals and animal-like protists that are at all likely to leave a fossil record, there are only 12 phyla and 31 classes in the present seas. That actually represents a slight decrease from the 13 phyla and 33 classes known for late Ordovician seas. The recent phyla are the same as those of the Ordovician. Several of the classes are of later origin and have replaced extinct classes present in the Ordovician. Replacement has been more and more complete at lower levels of the hierarchy of classification.

Why have some of the major groups become extinct? In assembling the data for this paper we have observed the following facts. It seems that several different basic patterns of morphology arose among the groups which, early in their history, had a number of short-lived primary subgroups, as for example the classes of the Echinodermata and the orders of the Nautiloidea. In each case, the "successful" pattern of morphology was exhibited only by the long-lived subgroups and was characterized by the development of numerous genera and species flourishing over a wide geographic area for a long period of time. Once the basic pattern had been established, subsequent modifications were relatively minor but numerous. In contrast, the basic morphologic patterns adopted by the short-lived subgroups (and a few of the long-lived ones) exhibited very few minor modifications and never became "successful" in the sense of being characterized by large numbers of genera and species and broad geographic range.

Completing our summary, we call attention to the fact that many groups of animals with calcareous skeletons show primary divergence most rapidly during the latest Cambrian and early and middle Ordovician. Exemplifying this phenomenon are the echinoderms, the tabulate and rugose corals, the bryozoans, the articulate brachiopods, the mollusks, the nautiloids, and the Paleozoic crinoids. Raymond (1939, pp. 34, 38–40, 42) noted that the Ordovician was a period of rapid development and evolution of calcareous-shelled animals, and our data confirm his assertions.

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